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BULLETIN

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Vol. 43 No. 11

BULLETIN

OF THE

TORREY BOTANICAL CLUB

NOVEMBER, 1916.

The development of the embryo and seedling of Dioscorea villosa

PEARL MABRY SMITH

(WITH PLATES 31–34)

INTRODUCTION

According to the standard manuals, *Dioscorea villosa* L. is the only North American species of the Dioscoreaceae, a family that is mainly tropical and subtropical in distribution. Bartlett (1910), however, considers the name *D. villosa* at once a misnomer and a possible source of confusion and error, and proposes that it be dropped. In his classification, the Dioscoreae of the United States are referred to five separate species; the one treated in the present paper he calls *D. paniculata* Michx.

The early discussions of the embryos and seedlings of members of this family are confined to the mature embryo and its behavior in germination, and were prompted chiefly by taxonomic considerations. Dutrochet (1835) says that the embryo of *Tamus communis* is at first globular, then pear-shaped; the slender part is the cotyledon, the swollen part the body of the embryo. He describes two cotyledons: the one, conical in form, remaining within the seed during germination; the other, so closely applied to the globular part of the embryo that it is distinguishable only after germination. The larger cotyledon persists until the middle of summer. Dutrochet also describes the structure of the aerial stem, whose fibro-vascular bundles are of the monocotyledonous type, but arranged in a ring. He thinks that this apparent mingling of monocotyledonous and dicoty-

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ledonous characters indicates that the genus is intermediate between the two classes, although he refers it to the Asparageae. Endlicher (1836, p. 157) notes a resemblance in stem structure between *Tamus* and *Aristolochia*.

Jussieu (1839) finds a structure corresponding to the "second cotyledon" of Dutrochet in the embryos of *Dioscorea villosa*, *D. cordifolia*, and *Rajania hastata*. However, he thinks it to be not a cotyledon, but a sheath formed by the growth of the cotyledon, its development being coincident with the elongation of the cotyledonary limb. In his classification the genera in question are placed among the Asparageae.

Beccari (1870*a*), in agreement with Dutrochet, concludes from his examination of the embryos of *Dioscorea bonariensis*, *D. brasiliensis*, *D. sinuosa*, *Rajania cordifolia*, *Tamus communis*, and *Trichopus zeylanicus* (*Trichopodium zeylanicum*) that the organ in question is a rudimentary cotyledon; he finds it present, with some variation in shape and size, in all the species named. Beccari also studied the germination of *D. bonariensis;* his description and figure agree substantially with Dutrochet's account of the process in *Tamus communis*.

The textbook of Le Maout and Decaisne (1873, p. 794) contains a figure of a longitudinal section of a germinating seed of *Tamus communis*, which shows very clearly the structures described by Dutrochet and others.

According to the view advanced by Strasburger (1872, pp. 317, 318), monocotyledons were derived from dicotyledons by the loss of one cotyledon. Obviously, if the Dioscoreaceae can be held to constitute a transition stage, or transition stages, between monocotyledons and dicotyledons, the "second cotyledon" might well represent a stage in the degeneration of one of the cotyledons of the latter group. Stimulated by these considerations, Solms-Laubach (1878) studied the embryology of *Dioscorea pyrenaica* and *Tamus communis*, the latter in some detail, but his results did not convince him that a second cotyledon was formed. However, he found a type of embryological development quite different from that which, since the work of Hanstein (1870), had been considered characteristic of monocotyledons. The growing point of the stem appears early in a terminal or nearly terminal position,

from which it is pushed aside by the development of the lateral true cotyledon. The so-called second cotyledon is, he thinks, merely a sheath. Both cotyledon and sheath are developed, however, according to Solms-Laubach, from a ring-shaped primordium.

Bucherer (1889) points out the additional fact that in *Tamus* not only the first secondary leaf, but all the secondary leaves, have similar sheaths. He also describes the anatomy of the mature embryo, and the processes of germination and of tuber formation. His account of the germination of the seed does not differ from the accounts of his predecessors.

MATERIAL AND METHODS

Material was collected in the vicinity of Madison, Wisconsin, at intervals of two or three days during the months of June, July, and August, 1913 and 1914. The flowers were fixed entire; when the ovules became sufficiently large, they were removed from the capsules before fixing. Later, the embryos were dissected out of the young seeds and then fixed. Difficulty was experienced in inducing the seeds to germinate, but germination was finally secured by keeping the seeds in soil out of doors all winter and bringing them into the greenhouse in the spring.

Strong and medium chrom-osmic-acetic acid solutions were used for all material of the embryo-sac and embryo which was to be sectioned; the stronger solution proved the more satisfactory. For embryos to be mounted *in toto* Carnoy's solution was used; for the seedling, a chrom-acetic acid solution, containing three tenths of a gram of chromic acid and seven tenths of a gram of acetic acid in each hundred grams of the solution, gave good results. The usual methods of hardening and embedding in paraffin were followed. Microtome sections were cut from five to seven microns thick.

Material containing embryo-sacs or early embryonic stages was stained with Flemming's triple stain. For the study of the later stages in embryo-development, Heidenhain's iron-alum-haematoxylin gave the best results. Some of the mature embryos were stained *in toto* with Delafield's haematoxylin. Staining with safranin and Lichtgrün proved useful in differentiating the tissues of the seedling.

THE EMBRYO-SAC

Two anatropous ovules are borne in each cell of the three-celled ovary and are pendulous on rather short funiculi. Beccari (1870*b*) figures the ovules in *Trichopus zeylanicus* as turned towards the axis of the pistil, but in *Dioscorea villosa* they are turned away from the axis.

At the time when the embryo-sac is fully organized (FIG. 1), the three antipodal cells have already begun to degenerate and fusion of the polar nuclei has taken place. Before the egg divides, its cytoplasm is highly vacuolate, and the nucleus occupies a position either approximately in the center or at the distal end of the cell. Both synergids persist, at least in some cases, until after the first division of the egg. When the embryo is somewhat older, only one structure is found beside it which I take to be a synergid. This structure (FIG. 5, *s*) sometimes forms a beak with faint longitudinal striations, which extends into the micropyle and corresponds closely in form and appearance with the "Fadenapparat" first described by Schacht (1856).

THE EMBRYO

The first division of the egg takes place only after several nuclear divisions have occurred in the endosperm. In an embryo-sac containing a two-celled embryo a count of the endosperm nuclei shows that five divisions have taken place, and the general appearance of the endosperm in other similar cases indicates that about the same number of divisions has occurred. In all cases observed, the plane of the first division of the egg is oblique (FIG. 2), approaching in a few instances the vertical (FIG. 4) or the horizontal (FIG. 5). The corresponding division is in an oblique plane in *Tulipa Gesneriana* (Ernst, 1901), and occasionally in *Avena fatua* (Cannon, 1900), and *Aglaonema* (Campbell, 1900). But in most monocotyledons, so far as has been reported, the plane of this division is transverse, as for instance in such forms as *Sagittaria variabilis* (Schaffner, 1897), *Lilaea subulata* (Campbell, 1898), and *Lilium philadelphicum* (Coulter, 1897). A transverse first division is found also in *Tamus communis* (Solms-Laubach, 1878), another of the Dioscoreaceae. The cells pro-

duced by this division in *Dioscorea villosa* are usually of about the same size (FIG. 4), but sometimes the basal cell is larger (FIG. 2). On account of the flattened shape of the seed it is possible to section the ovules always in the same plane. All figures of sections of the embryo are drawn from median longitudinal sections which are vertical to the plane of the cotyledon and which consequently afford a fair basis for comparison. In no case is a large vesicular basal cell formed, such as has been described in the embryos of the Najadaceae and Alismaceae.

The second division occurs in the basal cell, at right angles to the first wall (FIG. 3). Next, the terminal cell divides (FIG. 4); the position of the wall formed as a result of this division varies: in some embryos it is in the same plane as that of the second division (FIG. 4); in others, it is at right angles to the second wall, as in the embryo shown in FIG. 5, in which the third wall is nearly in the plane of the section and therefore cannot be shown in the figure. By either method, four similar cells are formed, as is the case in a few monocotyledons which have a massive proembryo rather than one of the filamentous sort that was formerly considered typical for the class. Quadrant formation has been observed in three genera of monocotyledons, *Lysichiton* (Campbell 1900), *Lilium* (Coulter, 1897), and *Erythronium* (Schaffner, 1901). It can hardly, however, be considered typical for the Dioscoreaceae, since in *Tamus communis* (Solms-Laubach, 1878) a filamentous three-celled proembryo has been described.

The next division may take place in one of the two distal cells or in one of the two basal cells. In the embryo shown in FIG. 5, the nucleus of one of the distal cells of a four-celled embryo is dividing; the wall separating the two distal cells is, as already noted, so nearly parallel to the plane of the section that it cannot be indicated in the figure. The spindle is at a lower focus than the resting nucleus shown.

In most cases, the second of the two distal cells of the four-celled stage now divides, so that a six-celled embryo is formed. Up to this time the embryo has not materially increased in size, but from now on there is a gradual growth. At the eight-celled stage (FIG. 6) the embryo is already noticeably larger, the size of the individual cells at this time being approximately equal to

that of the cells at the six-celled stage. At the sixteen-celled stage, the embryo assumes one of two typical shapes, each of which has been observed in several cases: it may be either elongated (FIG. 7), or nearly globular (FIG. 8). The exact sequence of divisions cannot be followed with any certainty after the eight-celled stage, nor is it possible to trace the development of the organs of the full-grown embryo from particular cells.

As the embryo develops a region is differentiated at the apex in which division is especially active, as indicated by the smaller size of the cells (FIG. 9, *m*). An elongation of the embryo, together with the increased rate of growth in its apical region, renders it a little later roughly pear-shaped (Fig. 10). The suspensor is now definitely marked off from the rest of the embryo (FIG. 10, *s*), and reacts differently to stains in this and succeeding stages. Now, too, the dermatogen is differentiated except on the side from which the first secondary leaf is to develop (FIG. 10, *l*; compare also FIG. 11, *l*). An embryo of the age of that shown in FIG. 10 bears a fairly close resemblance to one of *Lilium philadelphicum* figured by Coulter (1897, *pl. 34, f. 31*). Solms-Laubach (1878) shows no embryo of *Tamus communis* or of *Dioscorea pyrenaica* at a similar stage of development. Older stages than that of my FIG. 11 are represented in his figures only by drawings of surface views of whole embryos. According to Solms-Laubach's description the original terminal arch of the embryo becomes somewhat flattened and laterally displaced by the growth of one side of the embryo. From the flattened portion the plumule develops, surrounded by a ring-shaped wall of tissue. In my preparations of *D. villosa*, it appears clear that the lateral swelling shown at FIG. 11, *l*, which probably corresponds to that described by Solms-Laubach, is the primordium of the first secondary leaf, whose further development is shown in FIGS. 15–24. The growing point of the stem lies in the axil of the first secondary leaf, and it is obvious that both these structures are lateral in origin. The cotyledon (FIG. 11, *c*) develops in a terminal position. In *Tamus communis* and *Dioscorea pyrenaica*, according to Solms-Laubach, first the cotyledon and then the sheath develop from opposite points in the ring-shaped primordium, and are hence of lateral origin.

A careful study of serial sections of embryos of *Dioscorea villosa*, corresponding in size to those figured by Solms-Laubach, shows that no ring-primordium is formed, but that the first secondary leaf and cotyledon originate as limited areas of meristematic activity in an embryo which is still meristematic in all its parts; there is a very great increase in the size of the embryo as a whole after the first secondary leaf and the cotyledon have begun their development (FIGS. 15–24, all drawn on the same scale). The growing point of the stem consists merely of a group of cells in the axil of the first secondary leaf, and remains quite undifferentiated (FIG. 12, *g*) until germination occurs. The growth of the first secondary leaf is more vigorous at the start than that of the cotyledon (FIG. 15); but the latter soon begins to elongate rapidly, then expands to form a foliaceous structure which, in the fully-developed embryo, is peripherally very thin and flat, but is much thicker in the middle portion and at the base (FIGS. 13, 24). The first secondary leaf continues to swell out, then arches over and finally covers the growing point of the stem (FIG. 24). In the full-grown embryo, the edges of the base of the cotyledon extend for a short distance over the first secondary leaf, but by no means cover it (FIG. 13). A strikingly different structure has been described for embryos of other members of the Dioscoreaceae, which have a distinct sheath entirely covering the first secondary leaf. Beccari (1870*a*) finds this sheath entire in the genera *Dioscorea* and *Trichopus*, and two-parted in *Rajania* and *Tamus;* Solms-Laubach (1878) says that it is entire in *Testudinaria*. The short, thick suspensor persists to the time of the maturity of the seed (FIG. 13, *s*).

A vascular system, consisting of procambium strands, is present in the full-grown embryo of *Dioscorea villosa*. Cross-sections through the hypocotyl show a solid plerome cylinder which becomes a hollow cylinder at the base of the cotyledon. The hollow cylinder opens out into a trough-shaped mass as it passes into the cotyledon, then branches into three main bundles, which, in turn, branch profusely (FIG. 13). The first secondary leaf has a well-marked median bundle and two rather weakly developed lateral bundles. Bucherer (1889) describes but one vascular strand in the cotyledon of *Tamus communis;* in *Tamus*, however, the

cotyledon is tongue-shaped and not flattened. Bucherer also says that the primary root is endogenous and breaks through several rows of parenchyma cells when the seed germinates. No evidence of this condition has been found in *D. villosa*. There are no parenchyma layers outside the well-defined root-cap, which lies in immediate contact with the suspensor.

THE ENDOSPERM

As has been said, the polar nuclei fuse early and the primary endosperm nucleus undergoes several divisions previous to the first division of the egg; the nuclear divisions in the endosperm are simultaneous. The young embryo is at all times closely invested with a thick layer of endosperm cytoplasm. The endosperm makes rapid inroads on the nucellar tissue, using up all of it excepting two layers at the sides of the embryo-sac cavity and thicker masses at the chalazal and micropylar ends before cell division begins in the endosperm. Cell formation in the endosperm begins when the embryo has reached about the stage shown in FIG. 10. Tissue is formed at first throughout the whole of the cavity; later, but before the maturing of the seed, enough of this tissue is dissolved to form a large fissure in the central part of the seed which affords room for the rapid growth of the cotyledon at the time of germination. The cells of the endosperm contain abundant reserves of hemicellulose, protein, and oil. Dutrochet (1835) and Beccari (1870*a*) refer to the food material in the seeds of various Dioscoreaceae as "perisperm," but in *Dioscorea villosa* the material is clearly endosperm.

Formation of endosperm tissue is accompanied by, and is perhaps responsible for, certain changes in the contour of the seed and in the position of the embryo. When cell walls begin to form in the endosperm, nuclear division continues and is especially active in the region opposite the funiculus and adjacent to the embryo with the final result that this portion of the seed becomes proportionately larger than the other parts. As a result of this one-sided growth, the embryo, whose long axis at first corresponds to the long axis of the embryo-sac, comes to lie with its axis at an angle of approximately forty-five degrees to the long axis of the seed.

THE SEEDLING

In the mature seed, the embryo is very small in proportion to the size of the seed. On germination the cotyledon increases rapidly in size (FIG. 28, *c*), filling the entire fissure which has been referred to as formed within the endosperm, and remaining within it. The basal part of the cotyledon elongates, forming a trough-shaped petiole in whose hollow the first secondary leaf lies. The primary root elongates rapidly and soon begins to give off secondary roots. The first secondary leaf elongates, then arches itself until its tip becomes free from the seed coats. Beccari (1870*a*) says that in *Dioscorea bonariensis* the first secondary leaf is bent over so that the upper surface of the lamina lies against the petiole until the entire leaf emerges. In *D. villosa* the leaf is not bent over while in the seed, but assumes the position described by Beccari on freeing itself from the seed and retains it until it is well above ground. In the seedling illustrated in FIG. 28, the second, third, and fourth secondary leaves have already begun to develop.

The three bundles of the cotyledon fuse in the petiole to form a single massive bundle (FIG. 27) which extends the entire length of the petiole, is clearly recognizable in the hypocotyl (FIG. 26, *t*), and forms one of the poles of the tetrarch root (FIG. 25, *t*). This condition differs from that in *Tamus*, in which, according to Miss Sargant (1903), the symmetry of the root stele depends upon plumular traces alone. No traces of cambium, such as often occur in monocotyledonous seedlings, were found. Each secondary leaf has three bundles. Excepting the traces from the second and third secondary leaves, no vascular strands are present in the seedling that are not represented in the embryo by procambial tissue.

There are eight bundles in the hypocotyl (FIG. 26). The largest one (*t*) is continuous with the cotyledonary bundle. Of the remaining bundles, the three largest (*lt*) are continuous respectively with the three bundles of the first secondary leaf. The hypocotyl is short, as in most monocotyledons, so that the bundles of the hypocotyl converge rather rapidly as they enter the root and are consequently difficult to follow. It is evident, however, that branching of the phloem groups of the four main bundles

occurs, and that the branches fuse in pairs to form the phloem groups of the root. At the same time, a rearrangement of the xylem groups takes place, with the result that the protoxylem, which is external in the hypocotyl, becomes internal in the root.

CONCLUSIONS

Apparently the early divisions in the embryo of *Dioscorea villosa* have no very definite relation to the formation of organs or to the constitution of the embryo, since no important differences are found among the ripened embryos which might correspond to the observed differences in the plane of the first division or in the shape of the proembryo.

Widely accepted generalizations on the embryology of monocotyledons and dicotyledons have been based on cases such as *Sagittaria* and *Capsella* in which a filamentous proembryo is formed whose terminal cell gives rise to the cotyledon in monocotyledons and to the stem primordium in dicotyledons. However, as Coulter and Land (1914) have pointed out in the case of *Sagittaria*, the origin of organs from particular cells of filamentous proembryos has been assumed rather than proved. Moreover, a number of genera, both of monocotyledons and dicotyledons, have now been investigated in which the proembryo is massive. In several monocotyledonous genera, including *Zannichellia* (Campbell, 1897), *Lilaea* (Campbell, 1898), *Sparganium* (Campbell, 1899), *Avena* (Cannon, 1900), and sometimes *Limnocharis* (Hall, 1902), both cotyledon and growing point are found to originate from the terminal segment. However, a considerable amount of growth, resulting in a mass of tissue, must occur in the embryo before actual differentiation of organs takes place. If the positions of the primordia of the cotyledon and stem on this mass of tissue can be said to be terminal or lateral, this difference might serve as a basis for the distinction between monocotyledonous and dicotyledonous embryos. Unfortunately, it is at just this period of development that gaps in embryological studies are usually found. If position of origin be considered the criterion, the embryo of *Dioscorea villosa* is strictly monocotyledonous.

Lyon (1901) has advanced the view that an area extending entirely around the axis of the embryo is potentially cotyledonary.

The maximum development in this area takes place at the point or points that are in the most favorable position to function; in monocotyledons maximum development occurs on only one side, while in dicotyledons equal growth occurs at two points diametrically opposite each other. This notion has been further developed by Coulter and Land (1914) in connection with their work on some of the South African Liliaceae, particularly *Agapanthus*. Coulter (1915) even extends the generalization to gymnosperms. According to his view, a variable number of primordia appear on the cotyledonary ring; one, two, or more of these develop, the growth of the others being checked, principally by the growth of other organs of the embryo. As I have pointed out, no cotyledonary ring was observed at any time in the embryo of *Dioscorea villosa*, although such a structure has been described for *D. pyrenaica* and *Tamus communis* (Solms-Laubach, 1878). The two primordia that do appear in *Dioscorea villosa* develop into the cotyledon and the first secondary leaf respectively. The only way in which this case can be made to fit Coulter's theory is by assuming that the vigorous development of the first secondary leaf has entirely checked the development of the cotyledonary zone except at one point. However, the figures of Solms-Laubach (1878) indicate that the development of the first secondary leaf is just as vigorous in *Tamus*. I have no explanation to offer of the entire absence in *D. villosa* of a sheath covering the first secondary leaf, which is so prominent a feature in the embryos of other Dioscoreaceae.

There is so much diversity of opinion in regard to the phylogenetic significance of seedling anatomy that it seems hardly worth while to discuss the question to any extent in connection with *Dioscorea villosa*. Miss Sargant (1903) considers the tetrarch root such as is found in *D. villosa* primitive; however, in her opinion, this form of root structure is associated with the early development of the plumule which is characteristic of climbers. On the other hand, Hill and De Fraine (1913) consider diarch root structure primitive, but think that the root structure in any given case is largely dependent upon the size of the seedling. The seedling of *D. villosa* is small so that the formation of a tetrarch root cannot be accounted for on the basis of the size of the seedling. The

plant is a climber, however, and the structure of the root might be explained on that ground, thus losing its phylogenetic significance.

SUMMARY

1. The plane of the first division of the egg is oblique.

2. A spherical four-celled proembryo is formed.

3. The first secondary leaf is the first organ of the embryo to be differentiated. The growing point of the stem consists, up to the time of germination, of a group of cells in the axil of the first secondary leaf. Both structures are lateral in origin.

4. No "cotyledonary ring" was observed. The cotyledon originates in a terminal position.

5. No structure which is in any way comparable to a second cotyledon is present; the sheath which is described as covering the plumule in other Dioscoreaceae is wanting.

6. Abundant endosperm is present in the seed.

7. The growing point of the stem begins to give off secondary leaves soon after the seed germinates.

8. The root of the seedling is tetrarch; the hypocotyl is polyarch.

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UNIVERSITY OF WISCONSIN

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Description of plates 31-34

With the exception of FIG. 28, all drawings were made with an Abbé camera lucida, the drawing being at the level of the base of the microscope. Leitz oculars and objectives were used: FIG. 1, ocular III and objective 7; FIGS. 2–9, ocular III and objective 1/16; FIGS. 10–12, ocular I and objective 7; FIG. 13, ocular I and objective 3; FIGS. 14–24, ocular I and objective 4; FIGS. 25–27, ocular I and objective 6. The drawings have been reduced one fourth in reproduction.

PLATE 31

FIG. 1. Mature embryo-sac.

FIG. 2. Two-celled embryo.

FIG. 3. Three-celled embryo.

FIG. 4. Four-celled embryo.

FIG. 5. Four-celled embryo with one of the terminal cells in mitosis.

FIG. 6. Eight-celled embryo.

FIGS. 7, 8. Sixteen-celled embryos.

FIG. 9. Embryo somewhat older than those shown in FIGS. 7 and 8; region in which cell division has become especially active, *m*.

FIG. 10. Older embryo in which suspensor and body have become differentiated and which shows the first indication of the development of the primordium of the first secondary leaf, *l*; suspensor, *s*.

FIG. 11. Still older embryo in which the first secondary leaf, *l*, has begun development. The section was cut somewhat obliquely so that not all of the suspensor is shown; cotyledon, *c*.

PLATE 32

FIG. 12. Median longitudinal section through the fully-developed embryo, showing first secondary leaf, *l*, and the growing point of the stem, *g*.

FIG. 13. Surface view of the full-grown embryo; suspensor, *s*; first secondary leaf, *l*; cotyledon, *c*.

FIGS. 14–21. Series of outlines, all on the same scale, of median longitudinal sections of embryos, showing the development of the mature organs; first secondary leaf, *l*; cotyledon, *c*.

PLATE 33

FIGS. 22–24. Continuation of the preceding series, FIG. 24 showing the full-grown embryo.

FIG. 25. Cross-section through the primary root of the seedling; cotyledonary trace, *t*.

PLATE 34

FIG. 26. Cross-section through the hypocotyl of the seedling; cotyledonary trace, *t*; traces from the first secondary leaf, *ll*.

FIG. 27. Cross-section through the base of the petiole of the cotyledon.

FIG. 28. Seedling dissected out of the seed; first secondary leaf, *l*; cotyledon, *c*.

Further studies of the orange rusts of Rubus in the United States

L. O. KUNKEL

(WITH FIVE TEXT FIGURES)

INTRODUCTION

The writer's previous studies of the orange rust, showing that the *Caeoma* spores in material from New York, Illinois, Missouri and Wisconsin (6, 7) germinate like teleutospores, left the question as to the relationships of *Puccinia Peckiana* Howe unsolved.

Fischer (5) has recently tested the germination of the aecidiospores of the European *Gymnoconia interstitialis* (Schlecht.) Lagerh. He obtained long germ tubes having all the characteristics of ordinary aecidiospore germ tubes. No promycelia were observed and no cross walls were to be seen in any of the tubes. In one case a thinner tube that resembled somewhat a long sterigma developed at the end of a germ tube. This he thinks may have been the result of growth disturbances. Fischer also made infection experiments and obtained *Puccinia Peckiana* by sowing the aecidiospores on supposedly healthy plants of *Rubus saxatilis*. His results, taken in connection with those of Tranzschel (13), Clinton (3), and Liro (9), give strong evidence in favor of the view that *Caeoma interstitiale* Schlecht. and *Puccinia Peckiana* are connected. Fischer (5) explains the seeming contradiction between his results and those of the writer by assuming that we have been working with two different fungi. According to this view there would be two orange rusts on the blackberries of America: one the aecidial stage of *Gymnoconia interstitialis*, the other a short-cycled rust closely related to the genus *Endophyllum*. So far as known the short-cycled rust, which we may refer to under the name *Caeoma nitens* Burrill, does not occur in Europe. The fact that there, both are limited to the same low-growing wild species of *Rubus* is evidence in favor of such an assumption. *Puccinia Peckiana*, however, is not uncommon in several different parts of America, and we must expect to find its aecidial stage in these localities.

If there are, then, two orange rusts on the blackberries of the United States it would seem highly interesting and important to study them side by side in order to determine whether in addition to the difference in the way their aecidiospores germinate there are to be found morphological differences between the two Caeomas. The object of this paper is to bring the evidence which shows that we have two orange rusts on the American blackberries and to give a brief comparison of the two forms which have previously been confused and supposed to be one and the same rust.

OBSERVATIONS

It was in the hope of obtaining material for testing Fischer's assumption that the writer, at the suggestion of and in company with Professor R. A. Harper, made a trip to the White Mountains of New Hampshire. Here in the vicinity of the village of Glen the writer had on two previous occasions marked spots where the wild blackberry plants were infected with *Puccinia Peckiana*. On visiting these spots June 28, 1916, we found the plants well infected with a *Caeoma*. So far as we were able to determine macroscopically this *Caeoma* had all the characteristics of *Caeoma nitens*. The young infected shoots were chlorotic and somewhat taller than the normal ones. Many of the infected leaves were more or less deformed just as may be observed in the case of plants diseased with *Caeoma nitens*. Spermogonia were present in great abundance. Several infected plants and a considerable number of well-infected leaves were taken to New York City. The plants were put into flower pots and placed in a greenhouse, the purpose being to find out whether they would produce teleutospores later in the summer.

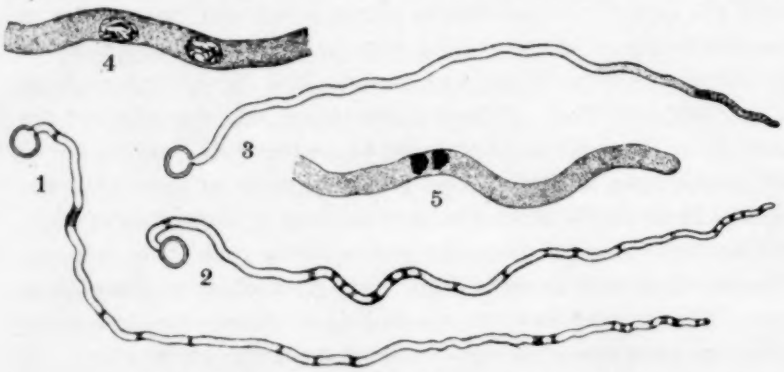
In order to test the germination of the aecidiospores they were dusted over the surface of tap water in Petri dishes. Twenty-one cultures were thus made and incubated at room temperature (about 25° C.). In twenty-four hours most of the spores had germinated. They produced long germ tubes having all the characteristics of aecidiospore germ tubes. No cross walls were to be found and no branches that might be taken for elongated sterigmata. The twenty-one cultures of germinating aecidiospores were carefully observed under the microscope and in only

one case must an exception be noted. One spore was found which had put forth a long germ tube that branched into two parts. On one of these branches two quite normal sporidia were borne on typically formed sterigmata. It is difficult to explain this case. Either the spore which gave the promycelium was a contamination or the aecidiospores of *Gymnoconia interstitialis* are in rare instances capable of functioning as teleutospores. The writer is inclined to the latter view.

In order to further test the germination of these aecidiospores a second sowing was made. This time the spores were dusted over the surface of three plates of tap water and three plates of Beyerinck agar. At the same time material of *Caeoma nitens* on *Rubus frondosus* Bigel. was brought into the laboratory from Van Cortlandt Park. These spores were also dusted over the surface of three plates containing tap water and three plates of Beyerinck agar. All of the cultures were made at the same time, on the same media and all were incubated at room temperature. A large percentage of the spores germinated in each of the cultures. The aecidiospores brought from New Hampshire produced long non-septate germ tubes that resemble in every way the germ tubes of other rust aecidiospores. Somewhat better germination was obtained on the agar than on the tap water, but the manner of germination was the same on the two media. The spores brought from Van Cortlandt Park gave practically one hundred per cent. germination and they produced in all cases promycelia.

Having used up all of the aecidiospores brought from New Hampshire in germination and inoculation experiments a second trip was made to Glen on July 7. This time the *Caeoma* was collected from three different localities and on two species of *Rubus*, namely, *Rubus canadensis* L. and *Rubus nigrobaccus* Bailey. Many cultures were made from the aecidiospores obtained from the three different localities. In each case a high per cent. of the spores germinated and they all produced long non-septate germ tubes like those shown in FIGS. 1 and 2. In order to study the nuclear behavior in the germ tubes a considerable quantity of germinating spores was fixed and stained according to a method outlined in an earlier paper (7). A study of the stained material shows that the long tubes typically contain two nuclei. These

nuclei lie close together near the end of the tube as is shown in FIG. 3. Sometimes they are separated by a distance of two or three hundred microns but they are never very far apart. The close proximity of the nuclei suggests that these germ tubes would give rise to sporophytic mycelium. The bases of the tubes appear quite empty while the protoplasm shows more and more density as we pass toward their apices. This is well shown in FIG. 3. The nuclei are strikingly large. They often show almost as great a diameter as the tubes that contain them. In some cases they have the appearance of ordinary resting nuclei with a distinct



GYMNOCONIA INTERSTITIALIS (Schlect.) Lagerh.

FIGS. 1 and 2 show the long unbranched aecidiospore germ tubes as they appear in the living condition, × 175. FIG. 3 shows a germ tube stained; the two nuclei lie near the end of the tube where the protoplasm is dense, × 175. FIG. 4 shows the nuclei in the resting condition; nuclear membranes and chromatin strands are clearly seen, × 590. FIG. 5 shows the deep-staining nuclei; nuclear membranes are not to be observed and chromatin strands are indistinct, × 590.

nuclear membrane and blue staining chromatin strands. Such nuclei are illustrated in FIG. 4. In other cases, however, it is difficult to make out a nuclear membrane; the chromatin strands are quite dense and stain so deeply that the whole nucleus appears a dark blue color. Such nuclei are illustrated in FIG. 5. In no case have nucleoli been observed and nuclear division figures seem to be absent from the preparations. One tube was found that had three nuclei, but this is a very rare case. The length of the germ tubes, the presence of only two nuclei, the large size of the nuclei, the absence of division figures and the lack of septa are all char-

acteristics which show that these spores in their germination function as aecidiospores. The appearance and behavior of the nuclei in the tubes is in striking contrast to what was observed in the study of the germination of the spores of *Caeoma nitens* (6, 7).

The germination tests show that the aecidiospores brought from New Hampshire function in an entirely different way from those collected in the vicinity of New York City. An experiment was next performed for the purpose of determining whether they would infect wild blackberry plants growing in this region and whether or not they would give rise to the teleuto-stage of *Gymnoconia interstitialis*. A number of plants of *Rubus villosus* Ait. and *Rubus argutus* Link found growing wild in the Bronx, New York City, were transplanted to flower pots and placed in a greenhouse. After they had recovered somewhat from wilting due to the cutting of the larger roots, nine plants of *Rubus villosus* Ait. and three plants of *Rubus argutus* Link, were placed in a moist chamber after being dusted with aecidiospores brought from New Hampshire. Unfortunately most of the spores had been used in the germination tests and only a limited quantity of the material was left for the infection work. An equal number of plants of each of the species used in this experiment were left uninoculated and served as checks. The plants were inoculated on the afternoon of July 1 and were left in a damp chamber for twenty-four hours. They were then placed in the open greenhouse beside the uninoculated plants. On August 15, all of the plants were carefully observed. One plant of *Rubus argutus* Link, was found to bear sori of *Puccinia Peckiana*. Only four leaves were infected but each of these showed numerous sori. All of the other plants appeared quite healthy and showed no signs of infection. It is difficult to understand why more of the plants inoculated did not become infected, but Liro (9) and Fischer (5) both report similar experiences with *Gymnoconia*. The check plants were all quite free of rust. Since *Puccinia Peckiana* has never been found on the blackberry plants in the vicinity of New York City we must assume that the plants brought into the greenhouse from the Bronx were free from this rust and that the infection obtained was the result of sowing the aecidiospores of the New Hampshire *Caeoma*. This experiment confirms the results of Tranzschel (13), Clinton

(3), Liro (9), and Fischer (5). Without a doubt, *Puccinia Peckiana* is the teleuto-stage of *Gymnoconia interstitialis*. The plants of *Rubus canadensis* L. that were brought here from New Hampshire bearing the *Caeoma* and planted out in flower pots were on August 15 found to be well infected with teleutospores of *Gymnoconia*. These results, together with the germination tests, seem to show conclusively that the orange rust common on wild blackberries in the vicinity of Glen, New Hampshire, is *Gymnoconia interstitialis*.

It seems proper to report at this point an infection experiment with *Caeoma nitens*. This experiment was performed in 1913 and 1914, but has not previously been reported. Sixteen plants of *Rubus villosus* Ait. found growing wild in Van Cortlandt Park were transplanted to flower pots and placed in a greenhouse. The plants were all quite free from rust infection and no infected plants were observed near where they were found growing. They were brought into the greenhouse the latter part of June. Ten of the plants were well dusted with the spores of *Caeoma nitens* and placed under bell jars for about one week. They were then placed in the open greenhouse. The other six plants were left uninoculated and were used as checks. No infection was observed on any of the plants during the summer and fall of 1913. In the spring of 1914, however, the young shoots of three of the plants that had been inoculated the preceding summer bore leaves well infected with *Caeoma nitens*. None of the check plants gave any infected shoots. The experiment shows that the spores of *Caeoma nitens* are capable of infecting new plants. It further shows that the *Caeoma* can reproduce itself without an intermediate stage. A similar experiment was performed in which the teleutospores of *Gymnoconia interstitialis* were used instead of the functional teleutospores (aecidiospores) of the short-cycled form. Ten plants of *Rubus procumbens* were inoculated by scraping teleutospores from mature sori with a wet knife blade and then smearing them over the surface of the leaves and young shoots. The plants thus inoculated were kept under bell jars for one week and then placed in the open greenhouse. They have been under observation for more than two years but the plants have not become infected. The viability of the spores was shown by germination tests and

the writer is unable to explain why infection did not result. The experiment should be repeated.

After being fully convinced that the orange rust, so common around New York City, is functionally different from the one in New Hampshire a special effort was made to discover possible morphological differences between the two forms. Infected plants from the two sources were placed side by side and carefully compared. Special notice was taken of the color of the spores in mass, the size and distribution of the Caeomas, the effect on the host, etc. Material of both forms was fixed in Flemming's weaker solution, embedded in paraffin in the usual way, sectioned with a microtome and studied under the microscope. Spermogonia are abundant in both cases. Their form, size and distribution was noted as well as the size and shape of the spermatia. In both forms the aecidiospores are born in chains with intercalary cells. The spores from the two sources were compared as to size, shape, content, thickness of spore wall and spore wall markings. Fifty ripe aecidiospores from the New Hampshire material were chosen at random and measured along their greatest diameters. The average diameter for the fifty spores was found to be 25.25 μ. Fifty aecidiospores of *Caeoma nitens* were likewise chosen and measured in the same way. Here the average diameter was found to be 25.29 μ. The difference obtained is not great and may well be attributed to errors in making the measurements.

This comparative study has failed to disclose either macroscopic or microscopic morphological differences between the two rusts. So far as the writer has been able to observe both are exactly alike morphologically. Only after having germinated the spores is it possible to distinguish between the two forms.

DISCUSSION

The close morphological and pathological similarity between two apparently different rusts at once raises the question as to whether or not they are genetically related. Do we have here a case of parallelism or has one of the Caeomas been derived from the other? It is possible to conceive that two rusts living on the same hosts may after a time show similar morphological characteristics, but it is hard to think they would become so much alike

as to be morphologically indistinguishable. If we consider only the life cycles of the two forms we find that they belong in groups that are rather widely separated in our classifications of the rusts. The short-cycled *Caeoma nitens* we would place near the genus *Endophyllum; Gymnoconia interstitialis* belongs near *Phragmidium*. Arthur (1) puts *Gymnoconia* in the Aecidiaceae while *Endophyllum* he places in the Uredinaceae. When we consider the two rusts from a morphological standpoint we find that in their *Caeoma* stage they are alike and we are inclined to consider them related forms. Werth (14) believes the aecidiospores of *Endophyllum Sempervivi* are capable of functioning either as aecidiospores or as teleutospores, according to the conditions under which they germinate. Maire (10) reports a variety of *E. Sempervivi* that regularly produces ordinary aecidiospore germ tubes. These suggestions are interesting in this connection and they deserve consideration in our studies of the two orange rusts. The finding of a basidium in cultures of the aecidiospores of *Gymnoconia interstitialis* offers a further suggestion and leads the writer to believe that the two rusts may be related. If a strain of the orange rust could be found in which some of the aecidiospores germinate by ordinary germ tubes while others produce promycelia the question as to the relationship of the two forms would be much clearer. An effort should be made to find such an intermediate strain.

The two Caeomas have undoubtedly been confused in this country. There is no way of knowing which rust Burrill (2) described as *Caeoma nitens* since it seems that both occur in the vicinity of Urbana, Illinois. Both are reported from Missouri and it is impossible to determine which form Newcombe and Galloway (11) used in their work. From their drawings of the germinating spores, however, one would guess that they had the short-cycled form. It is also probable that the material used by Olive (12) in his study of sexual cell fusions in the rusts was *Caeoma nitens*, but of this we can not be sure.

As one looks over the group of host species as given by Arthur (1) the question presents itself as to which ones are really host species for *Gymnoconia* and which ones are the host species of *Caeoma nitens*. This list undoubtedly includes the hosts of both

rusts and it is not possible in any given case to determine with certainty which rust was collected. Since *Gymnoconia* occurs on *Rubus saxatilis* and *R. arcticus* in Europe it seems natural to assume that the *Caeoma* on related species in this country belongs to *Gymnoconia*. It is probable, therefore, that the orange rust on the low-growing *R. arcticus* L. of Yukon, *R. stellatus* Smith of Alaska, and *R. triflorus* Richardson or *R. americanus* Britton of New Hampshire and Wisconsin will prove to be *Gymnoconia*. The writer has collected *Gymnoconia* on *R. frondosus* Bigel., *R. canadensis* L. and *R. nigrobaccus* Bailey. These are all upright-growing species and it may be that the orange rust on many of the other upright species is *Gymnoconia*. The writer feels inclined to think, however, that *Caeoma nitens* is the more common of the two rusts and that it will prove to have a wider range of host species than *Gymnoconia*. According to Clinton (3) the *Caeoma* has been reported from Carolina, Connecticut, Georgia, Illinois, Iowa, Kansas, Maryland, Massachusetts, Minnesota, Mississippi, Missouri, Nebraska, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Texas, West Virginia and Wisconsin while the teleuto-stage is reported from only four states: Illinois, Massachusetts, Missouri and New York. The orange rust in most of those states where the teleuto-stage has not been found is probably *Caeoma nitens*. New Hampshire, however, must be mentioned as an exception, since the rust common in that state has proven to be *Gymnoconia*. The fact that the orange rust is much more conspicuous than the teleuto-stage may to some extent account for its being more often reported. Only a careful study of the distribution and host limitations of the two forms in the several states can furnish grounds for definite conclusions. Nevertheless we may predict that the orange rust reported on *R. cuneifolius* Pursh, *R. occidentalis* L., *R. Randii* (Bailey) Rydb., *R. strigosus* Michx., *R. trivialis* Michx., *R. villosus* Ait., *R. vermontanus* Blanch. and *R. vitifolius* Cham. & Schlecht. is *Caeoma nitens*.

So far as is at present known the short-cycled orange rust does not occur in Europe. Before accepting this conclusion, however, a careful study of the manner of germination of the aecidiospores from various localities should be made. Special attention should be given to the *Caeoma* in those sections where

the teleuto-stage of *Gymnoconia* has not yet been found. Lageheim's (8) suggestion, "dass das *Caeoma* sich reproduciren kann," is interesting in this connection. He writes: "Aus mehreren Gründen scheint es mir nun nicht unmöglich, dass die Aecidien unserer Gymnoconia sich zu reproduciren vermögen. Während dieselben nämlich an vielen Orten des europäischen und asiatischen Russlands, im nördlichen, mittleren und südlichen Schweden und bei München gefunden worden sind, so sind die dazu gehörenden Teleutosporen (in Europa) nur bei Kuikkjokk im Schwedisch-Lappland, bei St. Petersburg und Moskau beobachtet worden." The orange rust of Europe seems to be of no economic importance and so far as the writer knows has not been found on cultivated blackberries or raspberries. This suggests that the rust so often reported as doing great damage to cultivated blackberries and raspberries in the United States is the short-cycled form. The writer has twice collected the orange rust on cultivated blackberries and in both cases it proved to be *Caeoma nitens*. It would be an interesting experiment to determine whether *Gymnoconia* is capable of infecting our cultivated blackberries and raspberries. This and many other experiments that suggest themselves must be left for future studies. Questions as to which of the two forms is the more primitive and as to what environmental conditions may have led to the development of two rusts with such different life histories and yet so much alike morphologically must at present be left unanswered. Both forms deserve further study.

SUMMARY

1. There are two forms of the orange rust on the blackberries of the United States. One is the *Caeoma*-stage of *Gymnoconia interstitialis* (Schlecht.) Lagerh.; the other is a short-cycled rust with a life history like the Endophyllums as described by Arthur (1).

2. The two rusts are morphologically alike in their *Caeoma*-stage though so different in their life histories.

3. The germination of the *Caeoma* spores is in the one case (*Caeoma nitens*) teleutoid, in the other (*Gymnoconia interstitialis*) it is just as typically aecidioid.

4. It is impossible at present to determine in the numerous references to orange rust of blackberries which form was under

observation except in a few cases where germination tests or infection experiments were made.

5. The short-cycled *Caeoma nitens* seems more widespread in the United States than *Gymnoconia interstitialis*.

6. It seems to be the short-cycled form of the orange rust that is so destructive to our cultivated blackberries and raspberries in this country.

I wish to thank Professor R. A. Harper for much helpful advice and criticism in connection with this work.

COLUMBIA UNIVERSITY

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The flora of Ladak, Western Tibet. I. Discussion of the flora

RALPH RANDLES STEWART

(WITH TWO TEXT FIGURES)

INTRODUCTION

In the books that deal with the "Trans-Himalaya" region there is the greatest confusion in the way the term "Western Tibet" is applied. The term may mean any place from the arid region, north of Sikkim, to the Karakoram Mountains, on the road to Turkestan. The result is that when the record "Western Tibet" appears in Hooker's Flora of British India (22)* one knows very little about where the specimen really came from. Even when the name of the collector is given, the source of the specimen cannot always be determined, as several explorers travelled extensively. As a result, a number of the species mentioned in the check list in the second part of the present paper may not grow in Ladak, but they are listed for the sake of completeness.

The region with which this paper deals is properly called Ladak to distinguish it from the other parts of Little or Western Tibet. Its inhabitants are largely Tibetan Buddhists and its flora is closely related to that of Tibet proper, but it is under the political control of Great Britain, being a part of the dominions of the Maharajah of Kashmir. Hemsley and Pearson's list of the plants of Tibet (20) does not include those from this region.

In their Flora Indica (23) Hooker and Thomson limit Ladak to a narrow strip on each side of the Indus, but I shall follow Neve's Tourist Guide (1913 edition).† According to Neve:—"Ladak is a large tract of country including Rupshu, Zanskar, Nubra, as well as Middle Ladak, and the lofty plateaux south of the Karakoram. It contains the loftiest inhabited districts in the world. No part is below 9,000 ft. and a large portion of the population live at

* The numbers refer to the Bibliography at the close of the second part of this paper.

† Neve, A. Tourist's guide to Kashmir, Ladakh and Skardo. 1913.

elevations of from 12,000 to 15,000 feet. While this is the height of the valleys and plateaux, the mountain ranges average from 17,000 to 21,000 feet and many peaks are 25,000 feet high."

In the check list of plants an effort has been made to list those reported from the region as given by Neve, using the "Great" or Snowy Range as the boundary on the Indian side, Baltistan on the west, the foot of the Karakorams on the north, Tibet on the east and also on the southeast.

One of the most characteristic features of Ladak is the Indus. The main caravan routes follow it or its branches and the villages are all placed so that they can get a little of its water for the fields. In fact, Ladak might be called the part of the drainage system of the Indus above 8,500 feet. The next lower part is called Skardo or Baltistan.

Contrary to the popular opinion, Tibet, including Ladak, is a very rugged country, rough, rocky and stony with countless mountain peaks and sandy desert valleys. The level places are either troughs between the mountains or the basins of extinct lakes. The further into the country one penetrates the more rounded are the hills and the gentler the slopes of the valleys, because of the smaller amount of erosion. There are many things that indicate that the Indus has been doing efficient work in clearing out the valleys near Kashmir, such as its deep gorges, the V-shaped valleys and the old marks of higher levels. Other great rivers are doing the same thing farther east.

Of the parts of Ladak visited, Rupshu is the least eroded. The whole country is above 15,000 feet and is extremely cold, barren and desolate. Springs are sometimes a day's journey apart and many valleys seem without any water. Many streams dry up before they reach a permanent river and in other places are shallow saline lakes, devoid of outlets. Despite its great altitude eighty flowering plants were found. There are practically no cryptogams. Both the flora and the topography resemble that of Tibet proper.

At the other extreme, Suru is supplied with much more water. The snow line is much lower and there are many streams and springs. The valleys in Suru are deep and the flora is more like that of Kashmir than that of Tibet. Dras is also more fertile than the rest of Ladak.

GEOLOGY

Although the geology of Ladak is not very well known, the following interesting facts are gathered from Burrard and Hayden (8):—

"All the geologic series is reproduced in Tibet from almost the earliest till modern times. Tibet, counting everything behind the great Himalayan range, consists of more than 20,000 feet of sediments, almost entirely of marine origin and represented by such rocks as slate, sandstone, conglomerate and limestone. Along its southern border it is in contact with the Himalayan granite which throws out branches ramifying through and metamorphosing the sediments.

"During almost all geologic time all of Tibet and the northern slope of the Himalayas was under a sea which at one time stretched to China and at another to the Mediterranean. The region kept subsiding and subsiding and later was elevated. In Cambrian times it is believed that Tibet and North America were joined, as the fossils are similar while they differ from those of Europe. At the close of the Cambrian this sea (the Tethys of Suess) linked up with the Palaeozoic sea of Europe.

"Crystalline and metamorphic rocks, granite, gneiss and schist cover the greater part of northern Kashmir, including Baltistan and west to the mountains of Afghanistan. To the east they run through northern Ladak. In eastern Kashmir they constitute much of Zanskar."

In view of the agreement among geologists that the elevation of the Himalayas has taken place in very recent time, and that Tibet, including Ladak, was under a sea which piled up tremendous sedimentary deposits until the Tertiary period, the flora can not be considered an old one. Nevertheless, the Russian botanist, Maximowicz (27), who worked on the plants of the untiring Tibetan explorer Prejevalsky, says that the flora is extremely ancient.

As the Workmans and other travellers have remarked, Ladak and Baltistan are lands of rock ruin. In the summer the heat in the daytime is so intense and it is so cold at night that the mountains are cracked and crumbling and there are huge talus slopes at their feet. Even in the winter Moorcroft reports that the heat may be intense for an hour or two in the sun, making a great daily variation in temperature.

CLIMATE

Ladak is almost cloudless in the summer time and the glare from the bare rocks and the sand is so intense that travellers must wear smoked glasses and pith helmets and must take especial care to protect the skin. Sun temperatures are so high that it is a wonder that any plant can live out in the deserts. India is

noted for its heat but the Workmans found that the sun temperatures in India rarely go to 170° F. At altitudes of 14,000–19,000 feet, however, they obtained maximum temperatures of from 183° to 204° F., although it was from 47° to 60° in the shade. The result is that one frequently finds it uncomfortably cool in the shade of a great rock while the sand is blazing hot in the sun.

The plants, therefore, that are not in damp places are exposed to extremes of temperature. This is true even in the winter time, for although a little snow falls, it does not lie long in the valleys. The missionaries at Khalotse, however, told us that the Indus remains frozen over during a part of the winter at least.

The growing season in Ladak is a very short one, even in the lower parts, and a traveller who visits the country only in July and August can therefore find the great majority of the species. There are several causes for this. In the first place, there is no rainy season to give birth to an ephemeral desert flora such as we have in the American Southwest. In the second place, plants that are in fruit at one altitude can be found in flower at higher altitudes. Further, most of the wild flora, excluding the annual weeds in the villages, is perennial and the leaves can be found even if the flowers are missing.

At Leh, Moorcroft reported that frosts began early in September and continued until May. Barley sown May 10th was cut September 12th. At Spituk, nearly 1,000 feet lower, he says that it took barley only two months to mature. Strachey says that in western Tibet elevations below 14,000 feet appear to be exempt from night frost for the greater part of the summer quarter. At 15,500 feet it freezes every night in the year. At 18,000–19,000 feet it thaws only during the afternoons of July and August. While we were in Rupshu in August we suffered greatly at night from the cold. One night half an inch of ice formed and the thermometer registered 21° F.

The country is practically without rainfall. The average at Leh is about three inches a year. Usually what precipitation there is falls at night and only on the mountain ridges and passes. A number of times in July and August we noticed that a light blanket of snow fell on the mountain tops while there was no

precipitation in the valleys. This is the reason that up to a certain altitude the number of species tends to increase instead of decrease. Even passes like the Fotu and Namika that are not near perpetual snow have more plants near the summit than in the deserts that have to be crossed in the ascent.

BOTANICAL EXPLORATIONS

Considering its remoteness, Ladak has been visited by a surprisingly large number of explorers who collected plants. This is due to the fact that it is on the only practicable highway from India to Central Asia, since Afghanistan is closed, and because it has been the base of a great deal of Tibetan exploration.

Despite its many visitors and the abundance of meager references the only attempt to bring together the work of the different visitors is that of the Flora of British India by Hooker (**22**) and here of necessity the plants are scattered through the seven volumes in their natural arrangement. Hooker never visited the Northwest Himalaya himself but we would be lost without his book. When we use Hooker's volume we are tempted to complain of the indefiniteness of many descriptions, the lack of keys to genera, and the "lumping of species"; but when we consider that he has done for British India what no one has done for the United States we are thankful indeed.

It is probable that the first Europeans to visit our region were the Jesuits, Desideri and Freyre, who passed through Ladak in 1714 on their way to Lhassa, but they have given us no botanical information. It was not until the expedition of Dr. Moorcroft, from 1819 to 1825, that we learn anything first-hand. In 1812 he had gained experience by penetrating into Tibet and exploring the region of the sacred Lake Manasarowar. In 1819 he started with Trebeck and Guthrie in an attempt to open up Central Asia to British trade. He entered Ladak from Lahoul, crossing over the Baralacha Pass and penetrating to Leh *via* Rupshu. He desired to press on to Turkestan, but although he waited about two years he failed to get permission from the authorities because of the jealousy of the Kashmir merchants. During his stay, however, he took time to explore Nubra, Zanskar, Dras and other parts of the country. He was not a botanist but he took a keen

interest in the agriculture of the people and the plants that might be useful elsewhere. Though his book (**29**) is nearly a hundred years old it is the best account of the crops and methods of cultivation. The few specimens he collected were sent to Wallich or Royle.

Vigne (**38**), who visited Kashmir, Astor, Skardu and Ladak in 1835, collected ninety species, but some were in such bad shape that Royle could not determine them.

Falconer, who was in charge of the Saharunpur Gardens, collected a little later (1839?) in Kashmir and Baltistan but he does not seem to have penetrated into Ladak any further than Dras.

The best collecting that has been done was probably by Thomas Thomson (**36**, **37**), from 1847 to 1848. He was botanist to the Tibetan Boundary Commission appointed by Lord Hardinge. Captain Henry Strachey, another keen observer, was in charge of the survey. Western Tibet was explored from Spiti to the Karakorams and large collections were accumulated which were widely distributed. Most of the Ladak specimens in the herbarium of the New York Botanical Garden were collected at this time.

In 1848, Richard Strachey (**35**) with J. E. Winterbottom, visited Lake Manasarowar and explored the Tibetan course of the Sutlej. This is really outside of Ladak but the flora is much the same. The next year, with his brother Henry, Richard Strachey went in from Ladak and explored Hanle and the Tibetan province of Guge. We are indebted to these three men for a great deal of valuable botanical and geographical information.

From 1855 to 1857 the Schlagintweit brothers (**32**) visited the Himalayas, crossing Ladak and going into Tibet. They were not botanists but they collected plants carefully and their collections have been worked up by different specialists.

About 1862, while on a pleasure trip, William Hay made a collection of Rupshu plants to which Hooker had access He does not seem to have published anything.

J. L. Stewart (**33**), about 1868, made a botanical tour through Rupshu and Ladak. Although he mentions some of his findings in his publications he did not publish a complete list.

In 1873 Henderson and Hume (**21**), members of the Forsyth Mission, published a list of four hundred and twelve plants col-

lected in Ladak and Yarkand. About two hundred and seventy-six of these are definitely listed from Ladak.

A great deal of our knowledge of the plants of Gilgit, Skardu, and the Karakoram is due to C. B. Clarke (12), although he does not seem to have done much, if any, work in Ladak proper.

J. F. Duthie crossed the Zoji in July, 1893, visited Dras, the Deosai Plains, and went back to Kashmir *via* Bandipur. In his reports (16) he does not list many of the plants he found.

A. Meebold entered Ladak from Kashmir *via* the Bhot Khol Pass in 1905 and explored parts of Suru, the Kangi region, and the road to Dah. He visited Leh and the Khardong, and has published interesting lists of plants (28).

A number of other men who collected in Ladak did not publish anything of their findings. Among these are Lance, Cayley, Stoliozka, and the Moravian missionaries, Heyde and Jaeschke. Hooker had access to most of these collections. Mention should also be made of the illustrated works of Royle (31), Jacquemont and Hoffmeister. The last two did not live to reach Europe and complete their work but Jacquemont's plants were published by Cambessedes and Decaisne (9), while Klotsch and Garcke (25) completed the work of Hoffmeister. Although none of these men visited Ladak they explored adjacent regions and their books are therefore very useful.

Recent lists of plants by Conway, Deasy, the Workmans and De Filippi of the Abruzzi expedition give us a good idea of the flora of the Baltistan and Karakoram region and are useful for comparison. The paper by Hemsley and Pearson on the Flora of Tibet (20), which covers the work of Thorold, Prejevalsky, Hedin and the other Tibetan explorers, is very valuable.

My own work was undertaken in 1912 and 1913. It covers Dras, Suru, Middle Ladak as far up the Indus as Upshi, and the region of Rupshu. The only districts that do not seem to have been collected in before are the Sapi, Rusi, and Yarungshan Passes in Suru and the obsolete road from Bosgo to Khalotse, *via* Tingmogung.

Itinerary of my trips.—I entered Ladak July 18, 1912, with three other men. We crossed the Zoji Pass (11,500 ft.) from Kashmir and followed the main caravan road to Leh (11,500 ft.),

arriving there July 30. August 2 we climbed to the Khardong Pass (17,500 ft.) but a snowstorm made it impossible to see what grew near the summit. This was the highest point reached in 1912.

Leaving Leh we returned to Kashmir by another route. From Bosgo we took the old and higher road *via* Timisgam and Tingmogung, rejoining the new road at Khalotse. August 14 we left the main path below Moolbeck and turned off toward Suru, crossing the Sapi La (16,000 ft.) on the 16th and visiting the Pakartse on the 19th. The 21st we crossed the Yarungshan La (15,500 ft.) and returned to Kashmir via the Wardwan Valley.

With another party I returned to Ladak in the same way (*via* the Zoji) in 1913 and arrived at Leh by the end of the month of July, staying a week in the vicinity. August 6th we started on up the Indus, passing the famous Himis Monastery and leaving the Indus at Upshi in order to visit Rupshu, reputed to be the highest inhabited part of the world. The inhabitants are nomads, depending for their livelihood on their herds of yaks, goats and sheep. From Gya we ascended the Takalung La (17,500 ft.) and descended to the plains that seem to be the favorite home of the wild ass, *Equus kyang*, and the Tibetan hare. August 9, we visited the salt lake called the Tsokar, one of the many Central Asian lakes without an outlet. August 12, we crossed the Lachalung La (16,600 ft.) and the Baralacha (16,000 ft.) the 15th, arriving in Kyelang, the main village of Lahoul, the next day. Thence *via* the Rotang and Kulu we went on to Simla.

Travelling on foot we covered about 400 miles in Ladak each summer. Not many novelties were found, though four or five things seem to be new. In order to make sure a trip to Calcutta or Kew would be necessary. With the exception of a few from Kargil (8,700 ft.) my specimens, which amount to about 475 species, were gathered at altitudes of from 9,000 to 17,500 feet.

FLORISTICS

Though the flora on the Indian side of the "Great range" of the Himalayas, which separates Kashmir from Ladak, is luxuriant and abundant, the opposite is true on the other side. In Kashmir, forests with *Betula utilis* at the upper limit are found up to about

13,000 feet but there is no forest in Ladak. Trees will grow when they are irrigated, or in a rare spot where they can find water naturally, but they form a very small part of the covering of the country.

Between Kashmir and Ladak there is, to be sure, a transition zone which is possibly widest in the Suru region, Himalayan alpine plants being found where there is water far into the heart of Tibet. Taking the flora as a whole, however, there could hardly be a more pronounced contrast than between these two regions. This is due not to altitude but entirely to water relations. The high mountains stop the rain-laden clouds and very little moisture gets across. Wherever there is enough water from melting snow, which can be led out by irrigation ditches to carefully prepared terraces, crops

FIG. 1. An oasis in the Rupshu region, altitude about 15,000 feet.

and trees flourish. Wheat or barley may be growing on one side of an irrigation ditch while desert plants are on the other. These ditches are prepared with great care and run along the hillsides for long distances. They are conspicuous objects because of the border of grass due to the extrat moisture.

There are, as Meebold also notes, three main elements in the flora of Ladak, alpine, desert and oasitic. These three are very easily recognizable and separable. The alpine element is largely

confined to narrow belts below the melting snows and along the upper courses of the streams and does not spread out into the valleys. The main part of the country is desert with a flora that connects up with Turkestan more than it does with India. The flora of the oasis (FIG. 1) is cosmopolitan. A few things like *Lancea tibetica*, *Pedicularis longiflora*, and species of *Gentiana*, which grow out in the desert if there is water, are indigenous without doubt, but most of the plants are weeds that may be native but are probably introduced. When a country has been settled as long as parts of Central Asia it becomes difficult to tell what the indigenous flora is.

If one unfamiliar with Ladak were to read through a systematic list of the species growing there he would suppose that the flora as a whole was mesophytic. This is chiefly because of the large number of weeds growing in the villages. As a matter of fact, most of the country is desert, but the number of truly xerophytic species is not proportionately large.

FOTU LA AND NAMIKA LA*

The following list of the plants collected on and near the barren Fotu and Namika Passes gives an idea of the type of plants that are found out in the open, away from the villages, at altitudes of from 10,000 to 13,000 feet. Even in this list there are a good many, such as the buttercups, the species of *Triglochin*, the gentians, the dandelion and the saxifrages, that grow only near springs in the desert.

Funaria submicrostoma
Ephedra Gerardiana
Triglochin palustris
" *maritima*
Pennisetum flaccidum
Agrostis alba
Bromus tectorum
Polygonum aviculare
Atriplex crassifolia
Eurotia ceratioides
Kochia prostrata
Silene Moorcroftiana
Ranunculus Cymbalaria
" *pulchellus*
Corydalis flabellata
Lepidum latifolium
Sisymbrium Columnae
Christolea crassifolia
Sempervivum acuminatum
Saxifraga sibirica
Potentilla anserina
" *bifurca*

* The Tibetan word "La" signifies Pass.

Potentilla multifida
Rosa Webbiana
Caragana pygmea
Astragalus Munroi
" *macropterus*
" *nivalis*
Oxytropis cachemirica
Epilobium Royleanum
Bupleurum falcatum nigrocarpa
Ligusticum Thomsoni
Primula sibirica
Androsace villosa
Acantholimon lycopodioides
Gentiana humilis
" *serrata*
Pleurogyne Thomsoni
Cynanchum acutum
Lindelofia Benthami
Eritrichium strictum?
Nepeta floccosa
Stachys tibetica
Lancea tibetica
Pedicularis longiflora
Rubia tibetica
Lonicera spinosa
Aster tibeticus
Erigeron andryaloides
Leontopodium alpinum
Chrysanthemum Richteria
Cousinia Falconeri
Scorzonera divaricata
Taraxacum officinale

SURU, YARUNGSHAN LA, SAPI LA, AND RUSI LA

Along the transition zone between Kashmir and Ladak almost any Kashmir plant that will live above 10,000 feet may be found, especially in Suru. Most of the plants are alpine mesophytes. Only 10 per cent. of these were also found in Rupshu, and they are forms like *Delphinium Brunonianum*, *Potentilla bifurca*, *Leontopodium*, *Taraxacum*, and *Aster heterochaeta*, which are widespread at high altitudes. Most of the plants in my list, that do not seem to have been reported before from Ladak, are from this transition region and are common Kashmir types. Examples are *Podophyllum Emodi*, *Lavatera Kashmiriana*, species of *Impatiens*, *Lotus corniculatus*, and *Astragalus frigidus*. The same may be said of the species from this region which were first collected by Meebold.

Coming from Kashmir, Meebold was impressed with the barren, Tibetan aspects of Suru, but going in the other direction later in the summer I was struck by the greater amount of green on the hillsides. While there are no forests and few trees, except willows, *Juniperus* and *Lonicera glauca*, there is much more herbaceous vegetation than in the rest of Ladak and everything indicates more moisture. This increased water supply is no doubt due to the presence of the Nun Kun peaks and glaciers. The greater

cloudiness, too, probably prevents the ground from drying out the way it does further into Ladak.

A list of plants from this region is given below. Definite stations will be cited in the second part of this paper.

Bryum tibeticum
Cystopteris fragilis
Juniperus macropoda
Ephedra Gerardiana
Andropogon Ischaemum
Panicum miliaceum
Phleum alpinum
Alopecurus himalaicus
Agrostis alba
Trisetum subspicatum
Poa annua
" *nemoralis*
Elymus dahuricus
Carex rigida
Juncus membranaceus
Salix daphnoides?
Polygonum affine
" *polystachyum*
" *tortuosum*
Axyris amaranthoides
Stellaria graminea
Arenaria Griffithii
" *foliosa*
Silene vulgaris
" *tenuis*
Lychnis apetala
" *nutans*
" *himalayensis*
Dianthus anatolicus
Aquilegia vulgaris pyrenaica
Delphinium Brunonianum
" *cashmirianum*
Aconitum heterophyllum
Aconitum Napellus multifidum
Anemone rupicola
Ranunculus pulchellus
" *hirtellus*
Podophyllum Emodi
Corydalis Gortschakovii
Thlaspi arvense
Draba glacialis
" *alpina*
Chorispora sabulosa
Sedum Rhodiola
" *asiaticum*
" *Ewersii*
" *tibeticum Stracheyi*
Sempervivum acuminatum
Saxifraga cernua
" *Hirculus indica*
" *Jacquemontiana*
" *flagellaris*
" *Stracheyi*
Ribes orientale
Potentilla Sibbaldi
" *fruticosa Inglisii*
" *bifurca*
" *argyrophylla*
Rosa Webbiana
Thermopsis inflata
Astragalus tibetanus
" *melanostachys*
" *himalayanus*
" *coluteocarpus*
" *frigidus*
" *rhizanthus*

Astragalus subulatus
Lotus corniculatus
Hedysarum microcalyx
Cicer songaricum
Geranium collinum?
Impatiens brachycentra
" *Thomsoni*
Lavatera kashmiriana
Hypericum perforatum
Epilobium latifolium
" *angustifolium*
Chaerophyllum acuminatum
Trachydium Roylei
Pleurospermum Candollii
Bupleurum falcatum
Acantholimon lycopodioides
Primula Stuartii
Androsace villosa
Gentiana Moorcroftiana
" *aurea*
" *tenella*
" *carinata*
" *decumbens*
Pleurogyne carinthiaca
Swertia cordata
" *patiolata*
Cuscuta capitata
Myosotis sylvatica
Scutellaria prostrata
Nepeta discolor
" *leucolaena*
Dracocephalum nutans
Phlomis bracteosa
Lamium album
Origanum vulgare
Elsholtzia densa
Verbascum Thapsus
Scrophularia scabiosaefolia
Lagotis glauca
Veronica delligera
Pedicularis tenuirostris
" *bicornuta*
Galium verum
" *boreale*
Lonicera glauca
" *asperifolia*
" *microphylla*
Campanula latifolia
" *aristata*
Aster heterochaeta
Erigeron alpinus multicaulis
" *alpinus uniflorus*
Leontopodium alpinum
Anaphalis nubigena
" *virgata*
Inula barbata
" *rhizocephaloides*
Chrysanthemum Richteria
Tanacetum artemisioides
Allardia glabra
" *nivea*
" *tomentosa*
" *Stoliczkai*
Artemisia amygdalina
" *salsoloides*
Senecio chrysanthemoides
" *arnicoides frigida*
Cremanthodium Decaisnei
Arctium Lappa
Saussurea Jacea
" *albescens*
" *sorocephala*
Jurinea ceratocarpa
" *ceratocarpa depressa*
Koelpinia linearis
Tragopogon pratense?

Taraxacum officinale parvulum *Lactuca decipiens*
Lactuca Scariola?

BARALACHA LA

Farther east, where Rupshu adjoins Lahoul, the plant life is very scanty because of the great altitude and because conditions of rainfall are very different from those in Suru. Lahoul itself is the transition zone to the luxuriant flora of the outer Himalaya. On the Baralacha Pass (16,000 ft.) scarcely twenty species were noticed, as shown by the following list. On each side of the Pass there is a very cold alpine lake that seems too icy for plant life. As early as 1820 Moorcroft wrote quaintly of one of them:—"Not a weed deformed its pellucid and tranquil waters. There seemed to be no fish in it, nor was any bird or even a fly in its vicinity."

Carex nivalis
Oxyria digyna
Polygonum cognatum
" *affine*
" *molliaeforme*
Stellaria decumbens
Silene Moorcroftiana
Dianthus anatolicus
Ranunculus hirtellus
Meconopsis aculeata
Corydalis meifolia
Draba lasiophylla
Sedum Rhodiola
Saxifraga sibirica
Potentilla fruticosa pumila?
" *argyrophylla leucochroa*
Nepeta glutinosa
Allardia tomentosa
Werneria nana affinis

RUPSHU

As mentioned earlier, the most Tibetan part of Ladak visited was Rupshu. Plants must grow there to an elevation of fully 18,000 feet, for we found half a dozen species at 17,500 feet. All of the plants listed, with possibly two or three exceptions, grew above 15,000 feet. Species of *Oxytropis*, *Potentilla*, and *Nepeta*, *Sedum tibeticum Stracheyi*, *Aster heterochaeta*, *Elsholtzia pusilla*, *Delphinium Brunonianum* and *Caragana pygmea* grew at the upper limit of plant life. On hillsides *Caragana* was the most conspicuous and abundant plant, spreading out on the ground in the way juniper does in the northeastern United States (FIG. 2). It furnishes the chief fuel in these lofty regions. The *Delphinium* is also a conspicuous plant with much the largest leaves and flowers of any plant near the top of the passes. The blades of its leaves may be

two inches in diameter. The wild rhubarb is the only Rupshu plant with good sized leaves. They are thick and very coriaceous.

The wind on the passes is so terrible that the plants that grow on the very top are prostrate and scarcely an inch high

FIG. 2. A shrubby pea, *Caragana pygmea* DC., the only conspicuous plant in large sections of Western Tibet, above an altitude of 14,000 feet.

with very small leaves and flowers. Examples are *Oxytropis densa*, *Potentilla bifurca*, *P. sericea* and *Nepeta longibracteata*.

Potamogeton pectinatus
Triglochin maritima
Stipa barbata
Deschampsia caespitosa
Poa pratensis
" *nemoralis ligulata*
Festuca rubra
Bromus crinitus
" *barbatus*
" *macrostachys*
Kobresia schoenoides
Carex Moorcroftii
Urtica hyperborea
Rheum spiciforme
Polygonum tortuosum
Polygonum sibiricum
Chenopodium album
Atriplex crassifolia
" *rosea*
Eurotia ceratioides
Salsola collina
Stellaria graminea
Arenaria musciformis
" *holosteoides*
Lychnis macrorhiza
" *brachypetala*
Isopyrum grandiflorum
Aquilegia vulgaris viscosa
Delphinium Brunonianum
Ranunculus pulchellus

Hypecoum leptocarpum
Corydalis crassifolia?
" *stricta*
Lepidium capitatum
Arabis tibetica
Alyssum canescens
Braya alpina
Christolea crassifolia
Sedum tibeticum Stracheyi
Sempervivum acuminatum
Saxifraga Hirculus indica
Potentilla tetrandra
" *fruticosa ochreata*
" *ambigua*
" *bifurca*
" *multifida*
" *sericea*
Caragana pygmea
Oxytropis densa
" *lapponica*
" *microphylla*
" *tatarica*
Biebersteinia Emodii
Pleurospermum stellatum
Primula sibirica
Gentiana aquatica
Marrubium lanatum
Nepeta longibracteata
" *nivalis*
" *tibetica*
Dracocephalum heterophyllum
Thymus Serpyllum
Elsholtzia pusilla
Veronica ciliata?
Rubia tibetica
Galium pauciflorum
Lonicera spinosa
Aster heterochaeta
" *tibeticus*
Leontopodium alpinum
Anaphalis nubigena
Tanacetum fruticulosum
Artemisia minor
Senecio arnicoides frigida
Werneria nana
Saussurea bracteata
" *glanduligera*
Taraxacum officinale
" *officinale parvulum*

NATIVE AND NATURALIZED SPECIES OF THE EASTERN UNITED STATES OCCURRING IN WESTERN TIBET

In comparing the flora of Ladak with a distant flora like that of the eastern United States there are many more similarities than one would suspect and it is possibly worth while to make a list of species that are common to both countries. Plant lists do not, of course, give a picture of a region, and the aspect of the two countries is absolutely different, but there are enough things similar to make an American feel somewhat at home.

At least 140 of the plants of Ladak, which amount to about 825 forms, occur here in America, too, but when one comes to examine them it appears that no less than 85 are weeds and not

native. As mentioned before it cannot be stated how many are introduced in Ladak. When one looks at the list of those that are native here it appears that nearly all are plants that like a great deal of water. An abundance of moisture is a great equalizer of environments and plants like Potamogetons, *Lemna* and Triglochins are very cosmopolitan. A smaller group consists of wide ranging temperate plants. There are therefore three groups of plants native to both countries: weeds, water-loving plants, and a few temperate cosmopolitan types.

NATIVE SPECIES

Cystopteris fragilis
Equisetum arvense
Juniperus communis
Potamogeton pectinatus
" *perfoliatus*
Zannichellia palustris
Triglochin maritima
" *palustris*
Milium effusum
Deschampsia caespitosa
Phragmites communis
Koeleria cristata
Catabrosa aquatica
Poa alpina
" *pratensis*
" *nemoralis*
Festuca rubra
Scirpus pauciflorus
" *rufus*
Eleocharis palustris
Carex stenophylla
" *rigida*
" *Goodenovii*
Lemna minor
Oxyria digyna
Polygonum aviculare
" *viviparum*
Polygonum Hydropiper?
Chenopodium hybridum
Corispermum hyssopifolium
Salsola Kali
Sagina procumbens
Ranunculus Cymbalaria
" *aquatilis*
Barbarea vulgaris
Cardamine pratensis
Braya humilis
Sedum Rhodiola
Saxifraga oppositifolia
Parnassia palustris
Potentilla Sibbaldi
" *Anserina*
" *fruticosa*
Astragalus alpinus
Epilobium angustifolium
Hippuris vulgaris
Primula farinosa
Glaux maritima
Limosella aquatica
Veronica Anagallis-aquatica
Utricularia minor
Plantago major
Galium Aparine
" *boreale*

NATURALIZED SPECIES

Panicum miliaceum
Setaria viridis
Heleochloa schoenoides
Alopecurus pratensis
Polypogon monspeliensis
Agrostis alba
" *canina*
Aira caryophyllea
Avena fatua
Eragrostis minor
Briza media
Dactylis glomerata
Poa annua
Festuca Myuros
Bromus tectorum
" *japonicus*
Lolium perenne
Agropyron repens
Salix alba
" *fragilis*
Populus alba
" *candicans*
" *nigra italica*
Urtica dioica
Parietaria debilis
Morus alba
Rumex Acetosa
Polygonum lapathifolium
" *Persicaria*
" *Convolvulus*
Chenopodium album
" *glaucum*
" *Botrys*
Atriplex rosea
Stellaria glauca
" *graminea*
" *media*
Cerastium vulgatum
Arenaria serpyllifolia
Dianthus deltoides
Saponaria Vaccaria
Aquilegia vulgaris
Berberis vulgaris
Lepidium ruderale
Sisymbrium Sophia
" *Thalianum*
Brassica juncea
" *nigra*
Sedum Rhodiola
Ribes Grossularia
Pyrus Malus
Trifolium pratense
Medicago falcata
" *sativa*
" *lupulina*
Melilotus alba
" *officinalis*
Lotus corniculatus
Geranium pratense
" *sibiricum*
Erodium cicutarium
Tribulus terrestris
Malva verticillata
Carum Carvi
Pimpinella Saxifraga
Convolvulus arvensis
Cuscuta europaea
Lithospermum arvense
Lycopsis arvensis
Lamium amplexicaule
Thymus Serpyllum
Mentha longifolium
Verbascum Thapsus
Veronica Beccabunga

Veronica agrestis
Galium verum
Gifola germanica
Tussilago Farfara
Arctium Lappa
Carduus nutans
Cnicus arvensis
Tragopogon pratense
Taraxacum officinale
Sonchus oleraceus
Lactuca Scariola

GENERA BEST REPRESENTED IN WESTERN TIBET

When we come to look at the commonest genera in Ladak, we find that only two are not represented in the eastern United States. These are members of the Compositae, *Allardia* and *Suassurea*. In addition, we have no native species of *Dianthus* or *Nepeta*. It is interesting to note that the genera such as *Tanacetum*, *Artemisia*, *Astragalus* and *Oxytropis*, which are more numerous in Ladak than in the eastern United States, are genera which are common in the Russian parts of Central Asia.

*Stipa**	*Chenopodium*	*Saxifraga*	*Lonicera*
Poa	*Stellaria*	*Potentilla*	*Galium*
*Bromus**	*Arenaria*	*Astragalus**	*Campanula*
Festuca	*Dianthus*†*	*Oxytropis**	*Erigeron*
Scirpus	*Ranunculus*	*Epilobium*	*Inula**
*Kobresia**	*Thalictrum*	*Primula**	*Tanacetum**
Carex	*Corydalis**	*Androsace**	*Allardia*†*
Juncus	*Sisymbrium**	*Gentiana**	*Artemisia**
*Allium**	*Draba**	*Nepeta*†*	*Senecio*
Populus	*Geranium**	*Veronica*	*Saussurea*†*
Salix	*Sedum**	*Pedicularis**	*Lactuca*
Polygonum			

* More species in western Tibet than in the eastern United States.
† No native species in the eastern United States.

PLANT ASSOCIATIONS

From the foregoing we have seen that most of Ladak is covered by open desert associations with bare ground between the individual plants. Many hillsides have so little soil and the summer heat is so intense that there is scarcely any vegetation at all. Sometimes a plant that would otherwise be sure to be eaten off can find a refuge beneath a thorny bush of *Caragana*, but as a rule they stand alone or in tufts.

Occasionally we find a modification of the desert flora. Where there is a spring on the mountainside and the water cannot drain away readily we get a continuous sod and a typical association of *Pedicularis longiflora* and species of *Triglochin*, *Carex*, *Gentiana*, and *Taraxacum*. The ground is often boggy in such situations and the water may be alkaline.

Alpine meadows are rare except in the transition zone near Kashmir. The places along the streams that may have been meadows ages ago have been made to grow a few food plants. Usually the streams are so swift that they are bounded by steep banks and there is very little opportunity for plants to gain a foothold or for a sod to form.

The oases which surround the villages contain practically the only trees, and these, with the exception of the *Hippophaë*, which is frequently used for hedges, are practically all introduced. The commonest trees are willows, poplars, walnuts, mulberries, apples and apricots. Small groves of the native juniper, *Juniperus macropoda*, are sometimes found. The commonest crops are barley, wheat and buckwheat. Our common garden vegetables do well and so do many of our common garden weeds.

Although there are no forests in Ladak, there are frequently thickets along streams and on little islands in the rivers. These have a typical association of the *Myricaria*, *Hippophaë*, *Rosa* and *Clematis orientalis*. These furnish shade for more delicate plants, such as species of *Veronica* and *Epilobium*.

INDEX TO AMERICAN BOTANICAL LITERATURE

1912-1916

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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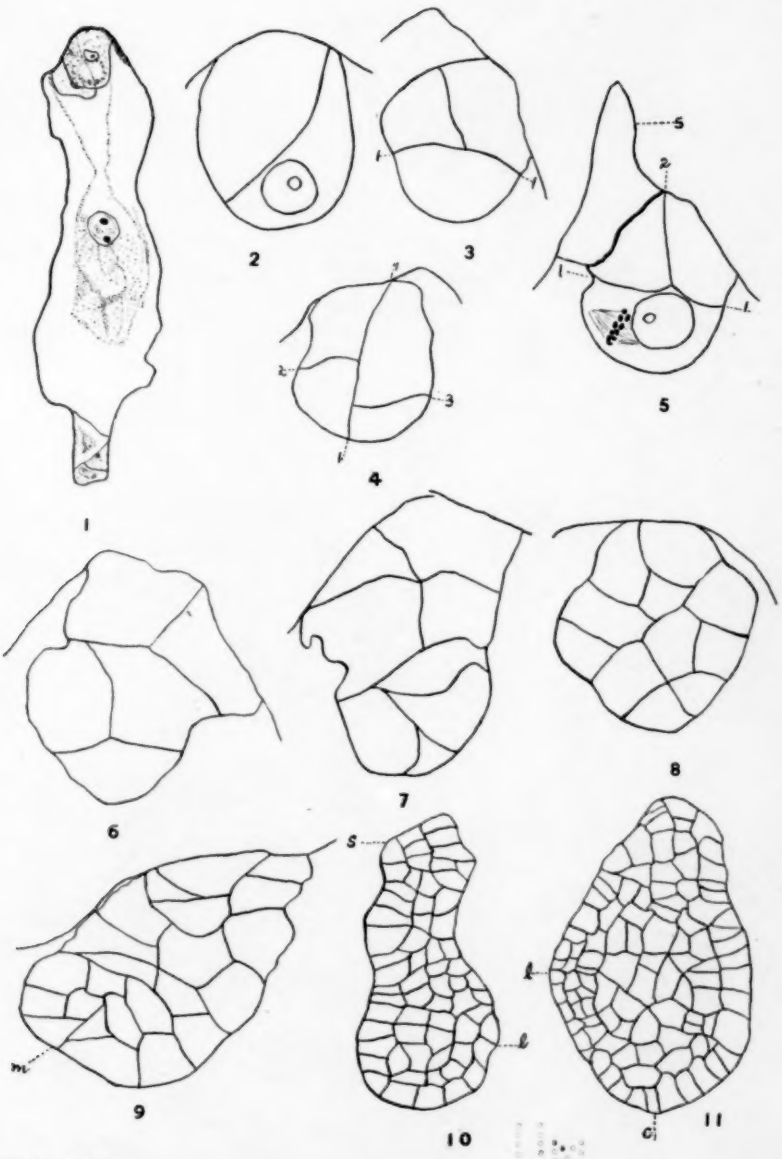

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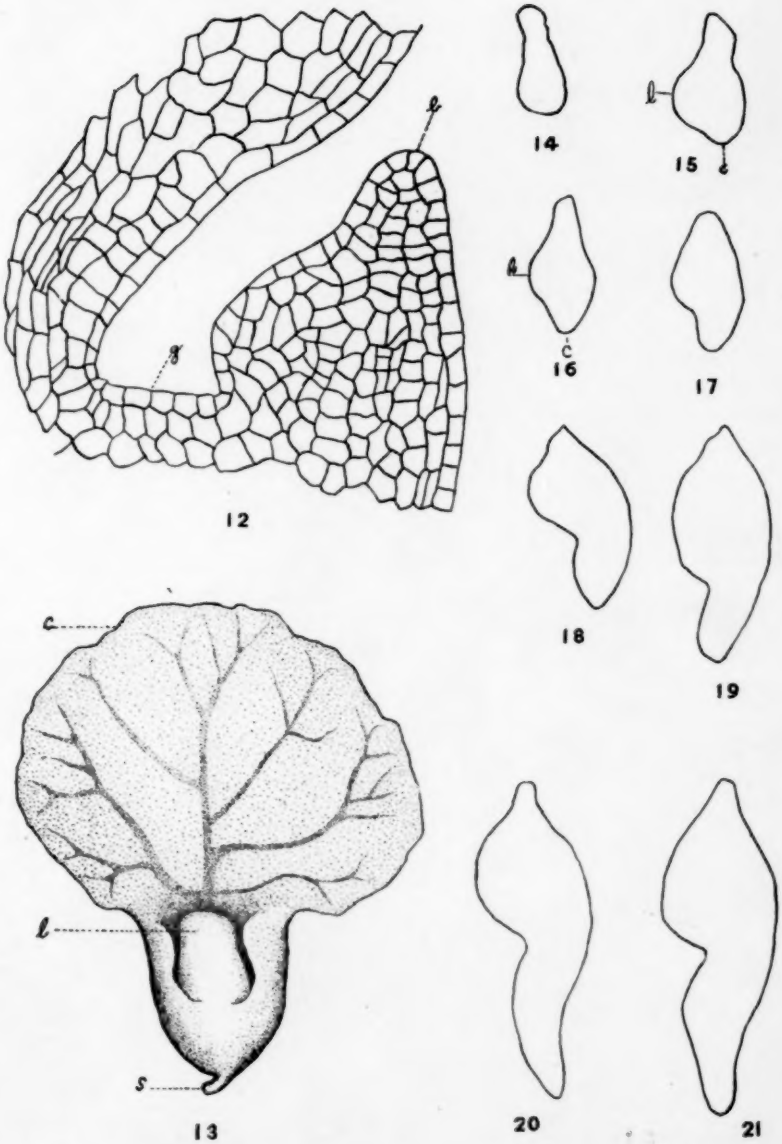

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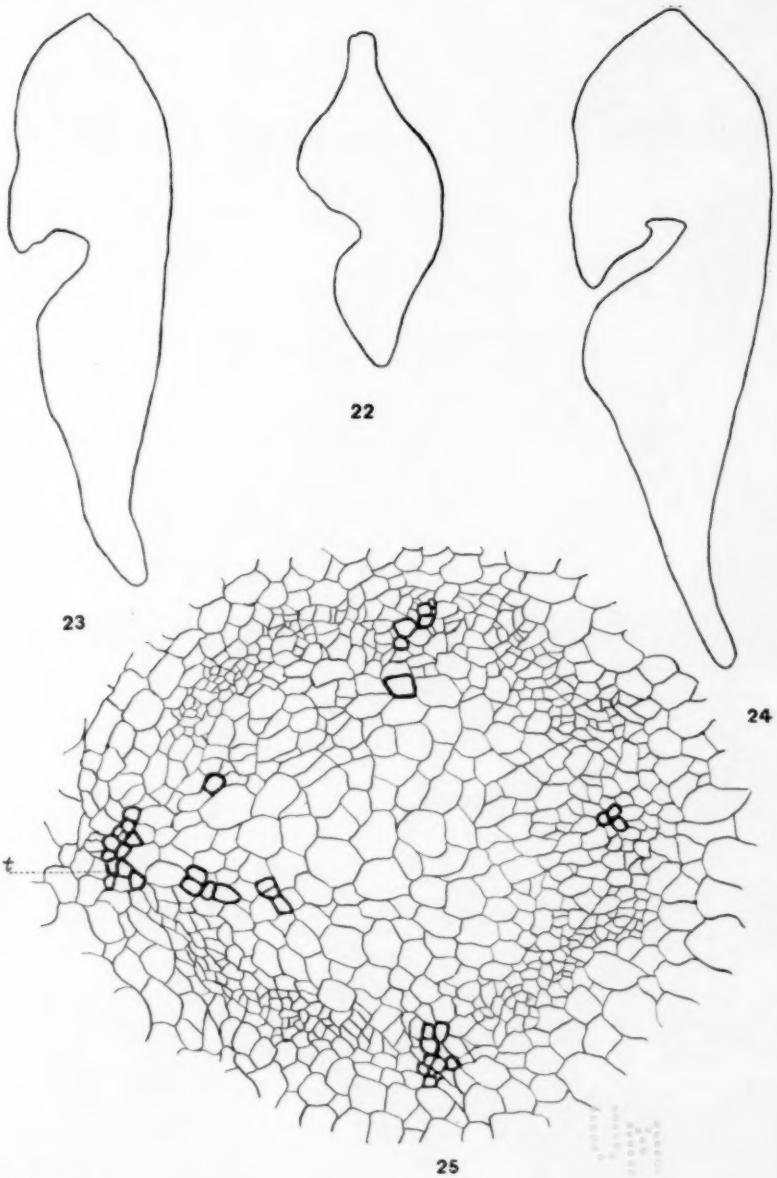

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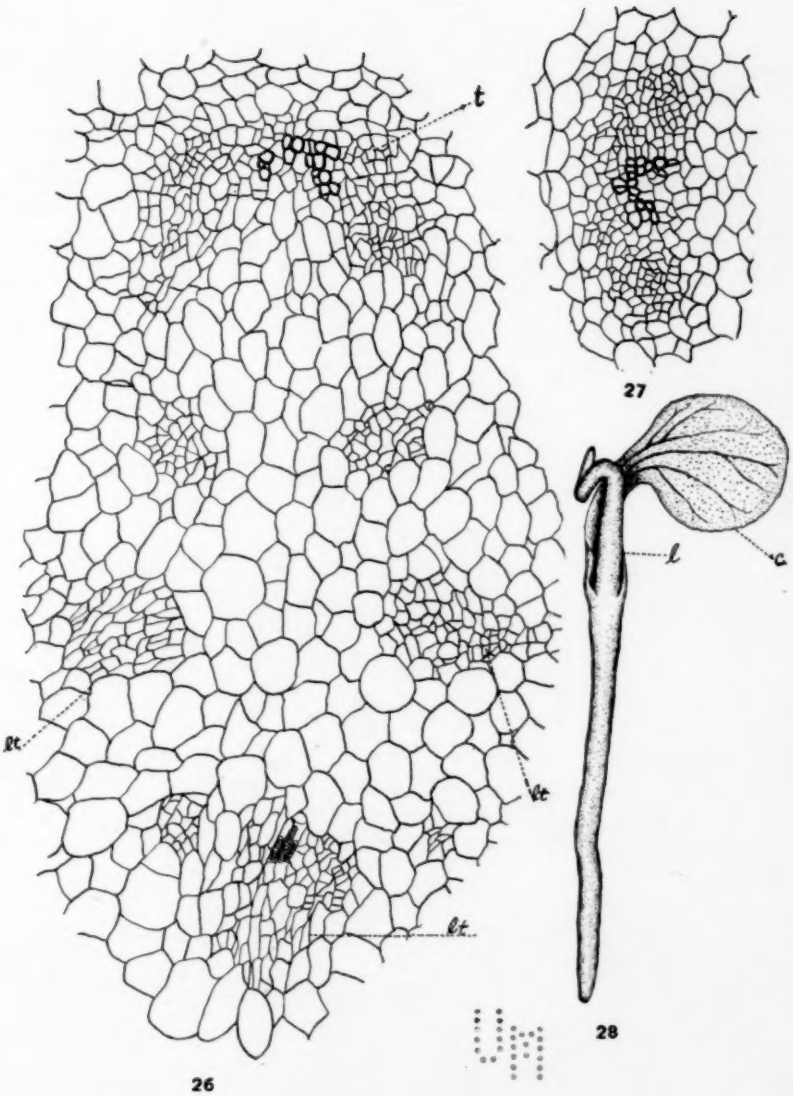

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